

Feature Review

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From Wild Type to Premium Cultivars: Selective Evolution of Key Trait Genes in Durian Domestication

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Abstract This study talks about the process of durian changing from wild state to the high-quality variety we eat now. The key point is how some key genes behind these changes are selected step by step by people. The study used several methods, such as population genome analysis, whole genome association analysis, and some molecular experiments. Together, these methods help us see a problem: how humans affect some important traits of the fruit, such as taste, disease resistance and yield, when selecting durian. The study also mentioned that these changes in durian cannot be explained by a single gene. There is a complex genetic structure behind them. Some are controlled by one gene, and some may be determined by many genes together. Some are “hard selection” and some are “soft selection”, and the traces they leave on the genome are also different. In addition, newly emerged mutations and existing gene mutations often work together. In addition to artificial selection, environmental changes and consumer taste preferences have also promoted the increasing diversification of durian varieties. This study not only allows us to better understand the genetic background of durian, but also provides important ideas and genetic resources for the future improvement of durian and other fruits.

Keywords Durian domestication; Selective evolution; Trait genes; Population genomics; Variety improvement

1 Introduction

Durian (*Durio* spp.) is often called the “king of fruits”. It is an important tropical fruit in Southeast Asia and has high economic value. In recent years, as people have become more and more fond of durian, many high-quality varieties have been cultivated in this region. These varieties not only provide more choices in the market, but also make the fruit traits of durian more diverse (Nawae et al., 2023).

The durian varieties we see today are actually domesticated over a long period of time. At first, they were wild durians. People planted and continuously selected types with good fruits, strong adaptability, and low disease resistance. This process is also constantly changing the genome structure and function of durian (Nawae et al., 2023).

The domestication of durian not only changed its appearance and taste. In fact, it also affected some important genes related to traits. For example, some genes related to gene regulation and protein action evolve faster in durian. Most of these genes are related to stress resistance and fruit development.

In addition, the differences between different durian varieties in certain genes are also obvious. Changes in gene copy number (CNVs) and the presence or absence of certain genes (PAVs) are particularly evident in some key genes, such as those related to disease resistance, flowering, and fruit ripening. These changes indicate that the genetic diversity of durian is very rich (Nawae et al., 2023).

This study is mainly to clarify how the key trait genes of durian were selected step by step during the domestication process. We also want to see how these changes in the genome have driven durian from the wild type to the current high-quality varieties. The study brings together the latest results of genome sequencing and comparative analysis, hoping to provide some theoretical and practical references for improving durian and breeding new varieties in the future.

2 Origin and Early Domestication of Durian

2.1 Wild relatives and geographical distribution

Durian (*Durio zibethinus*) originated in Southeast Asia. It is a very representative fruit in that area and an important economic crop (Figure 1) (Khaksar et al., 2024). Its wild relatives are mainly distributed in countries such as Malaysia, Thailand, Indonesia, Cambodia and Vietnam. The natural environment in these places is not the same, so the types and appearance of durian are also rich. Scientists use a method called “stable isotopes” and “element composition” to distinguish which country the durian comes from. This shows that durian is widely distributed in Southeast Asia, and durian in different places is also quite different (Zhou et al., 2021).

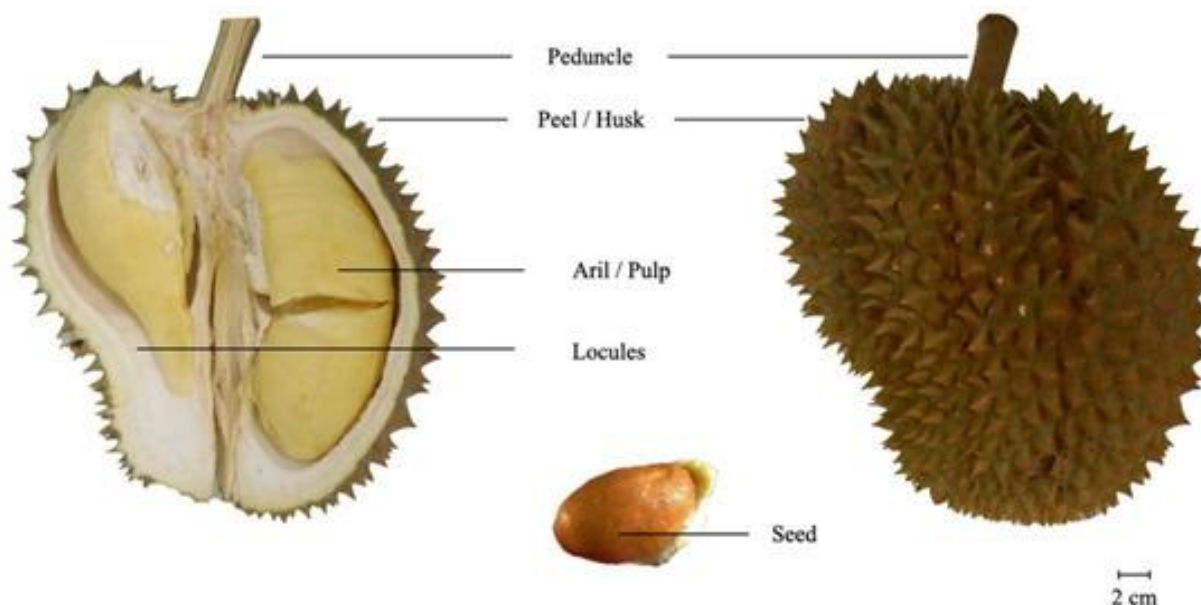


Figure 1 Images of durian (*Durio zibethinus* L.) fruit: peduncle, peel (husk), aril (pulp), locules, and seed (Adopted from Khaksar et al., 2024)

2.2 Archaeological and historical evidence of durian cultivation

Durian has a special taste and rich nutrition. People have been growing it in Southeast Asia for a long time. Although there is not much archaeological evidence of early durian cultivation, it can be inferred that people have long started to select and cultivate it from its widespread cultivation in Malaysia, Thailand and Indonesia (Aziz and Jalil, 2019). Because durian has a unique aroma and taste, it gradually became an important local fruit. Not only can it be eaten, it also represents a culture. Later, with the development of international trade, durian also slowly went to the world (Ali et al., 2020).

2.3 Initial selection pressures (environmental and human-driven)

The domestication process of durian is affected by both the natural environment and human selection. On the one hand, natural conditions such as climate, soil, pests and diseases will affect the growth of durian. These pressures have caused changes in durian in terms of disease resistance, flowering time, and fruit ripening speed (Nawae et al., 2023). On the other hand, people prefer durian with good taste, fine texture, and high nutrition. Therefore, when planting, varieties with strong characteristics will be specially selected for cultivation. Genome research has found that genes related to disease resistance, flowering, and maturity are different in different varieties, some genes have different numbers, and some genes have different expression strengths. These changes reflect that when humans select durian, they have deeply affected its genetic structure and function (Nawae et al., 2023).

3 Genetic Basis of Domestication in Durian

3.1 Overview of durian genome sequencing efforts

In recent years, great progress has been made in genome sequencing of durian (*Durio zibethinus* L.). Researchers have resequenced the whole genomes of three major varieties in Thailand: Kradumthong (KD), Monthong (MT), and Puangmanee (PM). They obtained 832.7 Mb, 762.6 Mb, and 821.6 Mb of genome data, respectively. In these

data, 92.4% to 95.7% of the core plant proteins were annotated. These results provide a good foundation for us to study the genetic diversity, gene family changes, and domestication-related genes of durian (Nawae et al., 2023). In addition, a research team in Hainan, China, also used RAD-seq technology to conduct genetic analysis of local durian germplasm. They also developed many SSR molecular markers, which can help breeding and gene positioning in the future (Lin et al., 2022).

3.2 Identification of major domestication-related genes

Through comparative genome analysis, researchers found that in certain specific gene families (such as families related to gene regulation and protein action, especially genes related to environmental stress), durian evolved relatively quickly. These changes may have occurred during the domestication process of durian in order to adapt to the environment and improve fruit traits. In a 2023 study, Nawae et al. found that in the Monthong variety, some genes related to flowering and fruit ripening (such as methylesterase inhibition-related genes) have different expression patterns from other varieties. These genes may have a great impact on the quality and development of the fruit. The SSR molecular markers developed by Lin et al. (2022) in Hainan also provide a useful tool for finding these important genes.

3.3 Comparison of genetic diversity between wild and cultivated durian

Lin's team conducted a population structure analysis of durian germplasm in Hainan and found that 32 genotypes can be roughly divided into two main subgroups. Some of the genotypes are very similar, which shows that the existing cultivated varieties are genetically close and have a narrow genetic base. In contrast, the researchers analyzed the genomes of several major cultivated varieties in Thailand and found that there are many genetic differences between them. Differences such as copy number variation (CNV) and the presence or absence of certain genes (PAV) are particularly evident in disease resistance genes and fruit development-related genes, indicating that they have high genetic diversity (Nawae et al., 2023).

4 Selection for Fruit Quality and Sensory Traits

4.1 Evolution of key genes governing fruit aroma and flavor

The special fragrance of durian mainly comes from a class of substances called “volatile sulfur compounds” (VSCs). The synthesis of these substances is related to some genes, especially genes like MGL (methionine gamma-lyase). When these genes increase in number and activity in durian, the fragrance will be more obvious. Studies have found that genes such as *MGL* and ethylene-related genes (such as *ACS*) are expressed more when durian fruits are ripe. This will also lead to the accumulation of VSCs and ethylene, resulting in the unique strong taste of durian (Teh et al., 2017). The metabolism of different durian varieties is also different. Some varieties have different contents of amino acids such as cysteine and leucine, which serve as precursors of fragrance. This change will also affect the final odor performance (Voon et al., 2007; Pinsorn et al., 2018). The differences in these metabolites and related genes provide a basis for us to select and improve the flavor of durian (Khaksar et al., 2024).

4.2 Regulation of sugar and lipid metabolism affecting taste

Whether durian tastes good, sweet or soft is largely related to changes in sugars and lipids. Studies have found that when durian matures, the sucrose content increases significantly. Some oligosaccharides, such as sugars in the raffinose family, were also detected to change for the first time at this time (Sangpong et al., 2021). In addition to sugar, organic acids also play a role. For example, malic acid and succinic acid increase when ripe, but citric acid has basically not changed. These acids and changes in sugars together determine whether durian tastes sweet or sour (Voon et al., 2007). In addition, genes related to lipid metabolism are also expressed more when ripe. This also makes the flesh more fragrant and tasty (Teh et al., 2017; Vallarino et al., 2023). Through the joint study of metabolome and genome, scientists can better pick out durian varieties with high sugar, high fat and good taste (Pinsorn et al., 2018).

4.3 Selection pressure on texture-related genes

The taste of durian flesh is also a point that consumers value very much. The texture is closely related to the changes in the cell wall when the fruit matures. Some “cell wall modification enzymes” play a key role in this

process, such as polygalacturonase and cellulase. Researchers found that when durian fruits mature, the expression of genes related to these enzymes will increase. This promotes the decomposition of cell walls, making the flesh softer and more dense (Sangpong et al., 2021). The different tastes of different durian varieties are likely due to differences in the expression of these genes and related metabolites. This shows that during the process of durian domestication and improvement, genes related to flesh texture have been affected by artificial selection (Voon et al., 2007; Teh et al., 2017).

5 Evolution of Disease Resistance and Stress Tolerance Genes

5.1 Genetic adaptations to fungal and bacterial pathogens

During the process of being cultivated and domesticated by humans, durian (*Durio zibethinus*) is often attacked by fungi and oomycetes. Pathogens such as *Phytophthora palmivora* and *Phytophthora vexans* can cause durian to rot or wilt, causing great economic losses. Because of the seriousness of this problem, growers and scientists have begun to pay attention to the disease resistance of durian. Commonly used methods now include agronomic measures, chemical fungicides and biological control. However, these methods are sometimes unstable and may also bring health and environmental risks. Now, some new molecular breeding methods are beginning to be tried. For example, by silencing certain genes (such as the gene that regulates protein phosphatase 2A), durian can be made more disease-resistant. In addition, some plant extracts also have antibacterial effects, and using them to prevent diseases may be safer and more effective than pesticides (Singh et al., 2024).

5.2 Abiotic stress resistance mechanisms in domesticated durians

In addition to the invasion of fungal and bacterial pathogens, durian also faces challenges from adverse environments such as drought and high temperature during its growth. In the past, people focused on disease prevention, but with the gradual strengthening of disease prevention and control, more and more studies are beginning to consider the impact of environmental stress on durian. Researchers are trying to use biotechnology to improve the adaptability of durian, such as gene editing technology, which can directly modify certain key genes of durian so that it can adapt to drought or high temperature environments to the maximum extent and grow normally, which is very helpful to ensure the yield and fruit quality of durian (Singh et al., 2024).

5.3 Trade-offs between disease resistance and fruit yield

In the durian breeding process, improving disease resistance often affects fruit yield to a certain extent. It is often the case that disease-resistant durian has a low yield or a worse taste. Therefore, making durian have a certain degree of disease resistance and produce a stable quantity and quality of fruit is a difficult problem in breeding. In order to solve this problem, researchers have tried to combine multiple methods, such as combining traditional management methods with molecular breeding methods, and it is possible to find a balance between disease resistance and high yield (Singh et al., 2024).

6 Flowering Time and Reproductive Traits in Domestication

6.1 Role of photoperiod and temperature in flowering control

When durian blooms depends largely on the environment, especially the conditions of rain and drought. Studies have found that if there is continuous drought for about 15 days, durian will begin to differentiate flower buds. The temperature has little to do with the time of the first flowering, so the effect of temperature on flowering is not obvious. On the contrary, changes in light duration and rainfall are the key factors (Eguchi et al., 2024). Not only durian, but also the flowering time of many crops is related to the photoperiod. Plants will “feel” the length of day and night, and then cooperate with the biological clock in their bodies to decide when to switch from growing to flowering. This mechanism helps plants adapt to different climates and growth environments (Wang et al., 2024).

6.2 Key genes regulating flowering time

In the domestication process of many crops, genes that control flowering time are the focus of attention. Genes such as the MADS-box family, *FT-like* genes and CONSTANS are often studied. They not only regulate flowering time, but also affect the structure and shape of flowers, thereby affecting the yield and adaptability of plants (Manrique et al., 2019). For example, in sunflower, the FT/TERMINAL FLOWER 1 gene family has multiple

copies and showed signs of being selected during domestication. This contributes to the formation of diverse flowering times (Blackman et al., 2011). Some *MADS*-box gene mutations have also played an important role in the improvement of reproductive traits in other crops (Schilling et al., 2018).

6.3 Pollination strategies and their influence on cultivar selection

Durian is difficult to self-pollinate successfully, and it has obvious self-incompatibility. Different varieties have different self-compatibility, some are completely incompatible, some are partially compatible, and some can self-pollinate but the effect is not good. Generally speaking, artificial pollination and cross-pollination with pollen from other varieties can significantly increase the fruit set rate and make the fruit better. If durian self-pollinates, the result is often deformed fruit, poor seed growth, and high abortion rate (Lim and Luders, 1998). After durian blooms, the time for successful pollination is very short, usually just one night. This period of time is synchronized with the lifespan of the flower itself, so pollination needs to be very timely (Honsho et al., 2007). Moreover, pollination with foreign pollen can not only affect fruit development, but also affect the quality of fruit and seeds through the so-called “cross-flowering effect” (Lim and Luders, 1998). During the domestication of crops, changes in pollination methods (such as whether self-pollination can be achieved) will directly affect the genetic diversity of the variety and its ability to adapt to the environment (Manrique et al., 2019).

7 Yield and Agronomic Performance in Cultivated Durian

7.1 Genetic modifications affecting fruit size and production

Fruit size and yield are two of the most important indicators in durian cultivation. These characteristics vary greatly between varieties. For example, the fruits of the “Monthong” variety are generally larger and heavier than those of the “Chanee”, which has a higher carotenoid content (Wisutiamonkul et al., 2017). During fruit development, several genes related to carotenoid synthesis (such as ZDS, LCYE, and LCYB) affect the color and nutritional value of the fruit (Wisutiamonkul et al., 2017). There are now studies using deep learning technology to automatically identify and measure durian fruits. Doing so can help more accurately grade fruits and estimate yields, and also help improve planting efficiency (Figure 2) (Barakat et al., 2023).



Figure 2 Durian sizing using SAM (Adopted from Barakat et al., 2023)

7.2 Hormonal regulation of fruit set and ripening

The growth and ripening of durian fruit are controlled by a variety of plant hormones. The most critical one is ethylene, which has a direct regulatory effect on fruit ripening. At the same time, auxin is also very important, and

it interacts with ethylene. Khaksar and Sirikantaramas (2020) found through research that a gene called *DzARF2A* is significantly more expressed in the late stage of fruit ripening, which can promote the expression of more genes related to ethylene synthesis and accelerate the ripening of the fruit. This performance is more obvious in durian varieties with faster ripening speed. There are also some genes related to hormone metabolism, such as *CYP88*, *CYP94* and *CYP707*, which belong to the cytochrome P450 family and are involved in the metabolism of hormones such as gibberellins, jasmonic acid and abscisic acid. The expression of these genes in different durian varieties is also different, and they may also be involved in controlling the ripening speed (Suntichaikamolkul et al., 2021). Ethylene can also affect the synthesis of volatile sulfides, thereby affecting the fragrance of durian (Pinsorn et al., 2024).

7.3 Selection for high-yielding cultivars in different regions

When breeding high-yield durian varieties, different places usually adopt different methods according to local conditions. Fruit thinning (removing some fruits) can make the remaining fruits larger, longer, and thicker in skin, and can also extend the shelf life. A common practice is to thin out 25% or 50% of the fruits. However, this method does not significantly increase the total yield (Nicolas et al., 2019). In the Mekong Delta in Vietnam, local fruit farmers cover the soil with plastic and use compound fertilizers rich in potassium, magnesium, and calcium to improve soil nutrients, reduce the problem of uneven fruit ripening, and thus increase the pulp ratio and sugar content, making the quality of durian better and the yield more stable (Quyen et al., 2025). In addition to these methods, there are now some new technologies that can be used to grade fruits, such as Raman spectroscopy and microfluidic paper chips. These tools can perform non-destructive testing and judge the maturity and quality without cutting the fruit, which can reduce post-harvest losses and improve the efficiency of the entire industry chain (Mettakoonpitak et al., 2024; Wattanasan et al., 2024).

8 Case Study: Selective Evolution of Key Trait Genes in ‘Musang King’

8.1 Background and historical selection of ‘Musang King’

“Musang King” (D197) is a very famous durian variety in Malaysia. It was selected from natural seeds at the end of the last century and has a history of more than 30 years. The flesh of this variety is golden in color, very soft to eat, with small seeds and a particularly strong fragrance. It is very popular in Malaysia and China. In the process of promoting this variety, people focused on selecting several characteristics, such as fragrance, edible rate (how much flesh), ripening performance (how many days to be delicious), etc. These characteristics gradually became the hallmarks of “Musang King”, which also shows that people selected these traits. As a result, the genes related to these traits were preserved in this variety and gradually fixed. This also promoted “Musang King” from a local fruit to a popular high-end durian.

8.2 Comparative genomics between ‘Musang King’ and other cultivars

Scientists used whole genome analysis methods to compare “Musang King” with other durian varieties. The results showed that its genes related to fruit aroma, taste and disease resistance were significantly different from those of other varieties. The most prominent one is the *MGL* gene family that controls the sulfur taste. In “Musang King”, the number of this gene family has increased, especially a copy called *MGLb*, which is expressed very highly when the fruit is ripe. This explains its particularly strong sulfur aroma. In terms of pulp taste, some genes related to cell wall degradation (such as *PG* and *PMEI*) in “Musang King” are expressed more strongly, which makes its pulp soften faster and more delicate when ripe. In terms of disease resistance, “Musang King” also has a different genetic structure. The number and arrangement of disease resistance genes such as *NBS-LRR* are different from other varieties. This shows that it has undergone selection for resistance during the breeding process.

8.3 Key genetic modifications contributing to premium fruit quality

The reason why “Musang King” is so delicious is related to the regulation of a series of key genes. The expansion and enhanced expression of the *MGL* gene are the reasons for its strong sulfur flavor. The two genes *ACS* and *LOX* affect ethylene and lipid metabolism, and also affect the fruit ripening speed and fragrance release. In terms of sugar content, genes such as *SPS* and *INV* are responsible for controlling the accumulation and decomposition

of sucrose, which directly determines the sweetness and taste of the fruit. Current research has found that these genes may have undergone genetic modifications such as selective pruning, promoter mutations, or copy number changes. These changes together form the molecular basis for the strong aroma and good taste of “Musang King”, and are also the key to its quality optimization during the domestication process.

9 Future Directions in Durian Breeding and Genetic Engineering

9.1 Potential of CRISPR and marker-assisted selection

As genome sequencing technology becomes more and more mature, molecular breeding has now become an important method for improving durian varieties. Molecular markers such as SSR (simple sequence repeats) and RAPD (random amplified polymorphic DNA) have been widely used in durian research. They can be used to analyze genetic diversity, identify different varieties, and assist in the selection of genes for good traits (Prihatini et al., 2016; Santoso et al., 2017; Siew et al., 2018). These tools also lay the foundation for gene editing technologies such as CRISPR. CRISPR can precisely modify specific trait genes. Doing so can speed up breeding and help us cultivate high-quality durian varieties faster (Nawae et al., 2023; Jantan et al., 2024).

9.2 Conservation of wild durian genetic resources for breeding

Wild durian has rich genetic resources and is an important material for future breeding innovation. Studies have shown that some local varieties show high diversity in both appearance and genes. In order to protect these resources, scientists recommend the use of in situ conservation plus selective breeding, retaining the population in its natural state while selecting individuals with excellent traits for breeding (Lin et al., 2022). In addition, technologies such as DNA barcoding and molecular markers can also help us better identify and classify wild durian. These methods can clearly understand the relationship between them and help organize and preserve resources (Sundari et al., 2021; Huy et al., 2023).

9.3 Challenges and ethical considerations in durian genome modification

Although gene editing and molecular breeding technologies have good prospects, there are still many difficulties in their actual application on durian. One problem is that the durian genome is very complex, with many structural variations and differences, which makes it difficult for us to accurately find and modify the target gene (Nawae et al., 2023). Another problem is that these technologies may bring some controversy. For example, genetic modification may affect the ecological environment, and consumers may not necessarily accept it. At the same time, it also involves biosafety and ethical considerations (Sundari et al., 2021; Huy et al., 2023). Therefore, in the process of promoting genetic modification in the future, we must not only continue to innovate in science, but also pay attention to ethical and social reactions and find a balance.

10 Concluding Remarks

Systematic research has found that during the domestication of durian, some genes related to fruit traits have changed. These changes are the result of long-term human selection. By analyzing the genomes of different varieties, researchers found that the number and presence of genes in durian in terms of disease resistance, flowering and fruit ripening vary greatly. Molecular markers such as SSR have been developed to help scientists identify and locate genes for good traits. These tools are very useful for breeding and germplasm resource protection. In terms of appearance and fruit traits, durian in different regions also has many differences. Although some varieties look similar, they are different in details such as thick peel, thick flesh, and length of fruit thorns. These differences provide a good reference for breeding good varieties. Pollinating animals such as bats are also critical to the yield of durian. They can help durian complete pollination and affect the quantity and quality of fruit. Protecting these animals can also help the durian industry develop more stably.

The current research results are very helpful for durian molecular breeding and future development. Through genetic diversity and molecular tools, researchers can find genes related to disease resistance, high quality and high yield more quickly. This can make breeding faster and more accurate. Studying the differences in durian traits and genetic structure can also better protect local varieties and prevent important genes from being ignored or lost. If pollinators are disturbed, durian production may decline. Protecting them is protecting productivity. This part also needs to be included in the long-term planning of the durian industry. In addition to the flesh, there are

many parts of durian that can be developed. Byproducts such as peels and seeds can be made into new products, increasing the added value of durian and driving broader bioeconomic development.

The next research can be deepened in several directions: continue to develop more useful molecular tools to make gene editing and seed selection more efficient. Strengthen the research on local varieties and wild durian to find more useful genetic resources. Learn more about the relationship between durian and pollinators, do a good job of ecological protection, and ensure that they can coexist for a long time. Try to make new products with durian byproducts, such as food, materials or other valuable things, to make the durian industry more environmentally friendly and more promising. The advancement of these directions will lay a more solid foundation for durian breeding and industrial development.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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